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Authors for correspondence:
Abigail E. Robinson
e-mail: aer13@bu.edu
Sean P. Mullen
e-mail: smullen@bu.edu

†These authors contributed equally to the study.

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Is temporal synchrony necessary for effective Batesian mimicry?

Abigail E. Robinson[1], Isabel Novick[1,†], Jessica Herrmann[1,†], Lily DeFelice[1,†], Aidan Engel[1,†], Dina Famin[1,†], Colleen Fetherston[1,†], Bianca Frintu[1,†], Julia Meyersiek[1,†], Musfika Mishi[1,†], Tran Gia Ha Nguyễn[1,†], Peter M. Buston[1], Thomas N. Sherratt[2] and Sean P. Mullen[1]

[1]Department of Biology, Boston University, Boston, MA 02215, USA
[2]Department of Biology, Carleton University, Ottawa, Ontario K1S 5B6, Canada

AER, 0009-0002-2397-7853; PMB, 0000-0001-5513-8259

Batesian mimicry occurs when palatable mimics gain protection from predators by evolving a phenotypic resemblance to an aposematic model species. While common in nature, the mechanisms maintaining mimicry are not fully understood. Patterns of temporal synchrony (i.e. temporal co-occurrence) and model first occurrence have been observed in several mimicry systems, but the hypothesis that predator foraging decisions can drive the evolution of prey phenology has not been experimentally tested. Here, using phenotypically accurate butterfly replicas, we measured predation rates on the chemically defended model species *Battus philenor* and its imperfect Batesian mimic *Limenitis arthemis astyanax* under four different phenological conditions to understand the importance of temporal synchrony and model first occurrence in mimicry complexes. We predicted that protection for mimics increases when predators learn to avoid the models' aposematic signal right before encountering the mimic, and that learned avoidance breaks down over time in the model's absence. Surprisingly, we found that asynchronous model first occurrence, even on short time scales, did not provide increased protection for mimics. Mimics were only protected under conditions of temporal synchrony, suggesting that predators rely on current information, not previously learned information, when making foraging decisions.

1. Introduction

Batesian mimicry is a classic example of adaptive evolution that occurs when a palatable mimic gains protection from predators by evolving a phenotypic resemblance to an unpalatable model species [1]. Mimetic relationships are maintained by predator behaviour, where theory predicts that predation rates on chemically defended prey decrease as predators learn to associate the warning signal of aposematic prey (and their mimics) with toxicity [2–6]. Therefore, protection from predation for the mimic is frequency-dependent and should break down in the absence of the model (see [7] for review). Previous studies of Batesian mimicry dynamics have confirmed these predictions (e.g. [8–10]), and revealed that factors including the palatability [11–14], alternate prey availability [15–18] and degree of mimetic perfection [19–22] strongly influence the efficacy of mimetic signals in deterring attack. However, while both laboratory- and field-based experiments have consistently demonstrated that protection for Batesian mimics is higher when mimics occur in geographic sympatry with their aposematic models [10,23–28], the importance of temporal synchrony (i.e. temporal co-occurrence) in maintaining Batesian mimicry, particularly in complex natural environments, has received less attention.

Batesian mimicry complexes are predicted to exhibit model first occurrence where models emerge seasonally before their mimics [29–31]. Models and mimics emerging together dilute the warning signal of the model, prolonging the learning process of predators and causing greater numbers of models and mimics to be sampled [32]. This implies that synchronized emergence (i.e. models and mimics emerging concurrently) is evolutionarily disadvantageous and that all participants in a mimicry complex (models, mimics and predators) benefit from temporal separation in the emergence of toxic models and their palatable mimics [29,33]. However, the optimal delay in emergence of mimics, relative to models and the role of temporal co-occurrence in natural environments is poorly understood.

The model first hypothesis has been investigated through theoretical models [29], analysis of long-term survey data [30,34] and targeted observation-based field experiments [31,35–37], and is supported in several dipteran–hymenopteran mimicry systems [30,31,38–40]. Conversely, some high-fidelity dipteran mimics have been shown to emerge before their hymenopteran models [36,41]. In this case, early emergence mimics may receive protection from predators that learned to avoid their aposematic models the previous year [35]. While experiments with insectivorous birds have shown that birds can retain learned avoidance of aposematic signals for one week [2,42], other work suggests that this avoidance can be retained much longer [43]. However, the available evidence for long-term predator memory retention in mimicry is limited. One long-term analysis of butterfly phenology shows that models will consistently emerge 3–15 days before their mimics, suggesting that model first occurrence may provide a selective advantage for mimics [34]. However, the selective advantage of the model first hypothesis has not been experimentally tested, and how long predators act on learned information about aposematic prey in natural environments when the model is not present (i.e. conditions of asynchronous model first occurrence) remains unclear.

Some mimicry complexes exhibit model first occurrence followed by temporal synchrony [31,34,38] while others appear to have model first occurrence followed by asynchrony, resulting in minimal overlap in flight time [31,35,44]. Elucidating how prey emergence timing and temporal co-occurrence influence predator foraging is necessary to understand how selection shapes phenology and the maintenance of mimicry, especially in areas near the model's range edge where the presence of the model becomes more unpredictable [26,27,45]. Predators may also continue to forage on toxic prey and their mimics under conditions of high physiological stress or when the toxic prey provides high nutritional value [46–49]. Ultimately, the adaptive value of different phenology strategies depends on the memory capacities, cognitive abilities, environmental conditions and foraging decisions of predators [6,28,35,50,51].

To investigate how the timing of mimetic prey emergence affects predator foraging, we conducted a large-scale field predation experiment using facsimile butterflies of the chemically defended species *Battus philenor* [42], its Batesian mimic *Limenitis arthemis astyanax* [52] and a palatable control *Junonia coenia*. At four spatially separated transects, we presented avian predator communities with facsimiles of both the model and mimic simultaneously (zero week, i.e. temporal synchrony) or with a one week, two week or four week delay between exposure to model and mimic facsimiles (i.e. asynchronous model first occurrence). Model and mimic phenology did not overlap during the asynchronous treatments. We predicted that mimics would experience the greatest protection against predation under conditions of one week asynchronous model first occurrence. Our prediction is based on three lines of evidence. First, previous research shows support for the model first hypothesis [29,31,34,38]. Second, while classical conditioning theory predicts that protection for mimics should decay over time in the absence of the model [6], naive predators have been shown to avoid models and their imperfect mimics one week after learning trials where the model was presented in high frequency [53]. Third, theoretical and experimental work show that predators are better able to distinguish between two similar phenotypes when they are presented simultaneously [54,55]. Our findings provide valuable insight into how phenology influences predator education about mimetic prey. We discuss the implications of these findings for the evolution of mimicry in nature.

2. Methods

(a) Field site

We conducted our field predation experiment at Quabbin Reservoir (42.38339° N, 72.31335° W) in central Massachusetts, USA (Permit Number: R-183). The Quabbin Reservoir is one of the largest protected areas in Massachusetts, with over 30 000 acres of avian forest habitat and over 200 resident bird species, including several insectivorous bird species [56]. We chose this site based on its location relative to the geographic ranges of the focal model (*B. philenor*) and mimic (*L. a. astyanax*). *Battus philenor* is common in the southeastern USA and becomes rare at latitudes above 41° N [57,58]. The Quabbin Reservoir is located at 42.38339° N latitude, approximately 160 km north of *B. philenor*'s range edge. *Battus philenor* is extremely rare in Massachusetts, allowing predation on the mimetic phenotype to be examined in an avian community that was naive to the warning signal of the model. All treatments were carried out between 21 May and 26 June 2021.

Predator community structure can vary over space and time, and this variation can correspond to changes in the survival of artificial prey that utilize different predator avoidance strategies [59]. Spatial and temporal variation in predator community dynamics can confound field-based predation experiments. To account for this, we used data from *eBird*, an open-source checklist-based citizen science platform, to analyse spatial and temporal variation in the predator community of the Quabbin Reservoir, an *eBird*-designated 'Important Bird Area' [60]. We used the Avian Diet Database to identify bird species whose typical diet contains 5% adult Lepidoptera, at minimum (i.e. 'insectivorous birds') [61]. To account for spatial variation in the predator community, we ran a spatial autocorrelation on the number of predator attacks across field sites using the pgirmess package (v. 2.0.3) [62]. All analyses were performed using R statistical software (v. 4.4.1) [63]. We also calculated the 95% kernel density home ranges across the Northeastern USA for all insectivorous birds present in the Quabbin Reservoir during our

experiment using the adehabitatHR package (v. 0.4.21) [64]. To account for temporal variation in the predator community, we analysed fledgling and migration dates using *eBird* data and checklists from the Athol Bird and Nature Club [65]. We then prepared Bray–Curtis similarity (BCS) matrices by day using the vegan package (v. 2.6.6.1) [66], and performed a perMANOVA across experimental time periods (adonis2 function; permutations = 999 [66]). To account for variation in observer effort, we divided total species observations per day by the number of observers present and prepared BCS matrices based on that data.

(b) Transect arrangement and data collection

Using fake butterfly replicas (facsimiles), we conducted four treatments with varying degrees of model first occurrence to directly test predictions about the relative importance of model first occurrence and temporal synchrony for predator learning in the context of mimicry. All treatments were restricted to 4 days, as previous work has shown that avian attacks on facsimiles decline significantly after this interval [23,67]. The first treatment replicated conditions of complete temporal synchrony (i.e. zero-week treatment, T0) where facsimiles of the model and the mimic were placed in the field at the same time, giving predators no time to learn the aposematic signal of the model before encountering the mimic. The second treatment tested conditions of one week model first asynchrony, where facsimiles of the model were placed in the field, removed after 4 days and facsimiles of the mimic were placed in the field one week after the model facsimiles were initially placed (i.e. one-week treatment, T1). The third and fourth treatments follow this design with a two-week gap (T2) and a four-week gap (T4) between placement of model and mimic facsimiles.

We also placed facsimiles of the control, *J. coenia,* alongside the model and mimic facsimiles in each treatment. *Junonia coenia* is a common palatable butterfly. Using facsimiles of *J. coenia*, we can control for spatial differences in avian population density or foraging frequency by directly comparing attack rates on mimic facsimiles to attacks on their respective control [9,23]. All four treatments were carried out in spatially separated sites at Quabbin Reservoir between 21 May and 26 June 2021 (see figure 1 for a map of site locations and experimental timeline; electronic supplementary material, table S1 for a detailed timeline of each treatment). Treatments were conducted along linear transects containing 20 sites (80 sites total) with 25 facsimiles of each species in each site (figure 1). Sites were separated by approximately 250 m, which exceeds the average avian predator home range size, allowing sampling of independent predator communities [9]. Start and end points were marked for each site using Garmin eTrex 10 and 22x GPS units to ensure the same locations were used for training and testing phases. Asynchronous treatments (figure 1; electronic supplementary material, table S1: T1, T2, T4) involved separate training phases (model and control) and testing phases (mimic and control), and thus had two control groups, resulting in 7500 facsimiles across both synchronous and asynchronous treatments (figure 1). Within sites, facsimiles were separated by approximately 2 m and attached to appropriate foliage with dorsal surfaces exposed to resemble butterflies engaging in territorial and basking perching behaviours [70,71]. Facsimile density was consistent across all four treatments.

(i) Training phase

Each asynchronous treatment involved a training phase where naive predators were trained with facsimiles of the toxic model. In each site, 25 facsimiles of *B. philenor* (unpalatable model) and 25 facsimiles of *J. coenia* (control) were placed on alternating sides of the transect, resulting in 3000 facsimiles in the initial training phase. All training phase treatments were conducted between 21 May and 16 June 2021 (see electronic supplementary material, figures S1 for specific dates). Training phases were conducted along transects in separate parts of the Quabbin Reservoir with consistent habitat composition across sites; T4 was conducted in sites 1–20, T2 was conducted in sites 21–40 and T1 was conducted in sites 41–60. During each training phase treatment, facsimiles of *B. philenor* were painted with a 2% Bitrex (denatonium benzoate) solution to educate avian predators by simulating the chemical defence of *B. philenor*. Bitrex is a non-toxic and extremely bitter compound commonly used in predation experiments to simulate avoidance learning [72–75]. When predators attack facsimile abdomens, the bitter taste drives learned avoidance [74]. Bitrex was reapplied daily, and facsimiles were removed from the field 4 days after placement. Facsimile clay abdomens were examined daily for evidence of bird attacks. Clay abdomens are often used in field predation experiments because they allow predators to leave impressions in the clay when they attack [76,77]. This method allows us to distinguish between avian and non-avian predation; bird attacks typically resemble deep, triangular bite marks or jagged puncture marks (electronic supplementary material, figure S1). Suspected avian attacks were recorded and photographed. Missing abdomens were not recorded as evidence of predation. Once data were recorded, abdomens were smoothed over or replaced to remove predation evidence. Photographs were later evaluated by two researchers and categorized as ‘avian predation’ or ‘not avian predation’. Photographs with non-avian predation marks (e.g. lizards or small mammals) were removed from the study. Only one predation event was recorded per facsimile per day.

(ii) Testing phase

After establishing that the native predator community learned to avoid facsimiles of the toxic model during the training phase, we conducted testing phases for all asynchronous treatments and the temporal synchrony treatment concurrently between 19 June and 26 June 2021 in the same sites where each corresponding training phase took place. Each asynchronous treatment involved 25 facsimiles of *L. a. astyanax* (undefended mimic) and 25 facsimiles of *J. coenia* (known, palatable control) per site (figure 1). The temporal synchrony treatment involved 25 facsimiles of the defended model (*B. philenor*), 25 facsimiles of the undefended mimic (*L. a. astyanax*) and 25 facsimiles of the known, palatable control (*J. coenia*) per site (figure 1). Facsimiles of

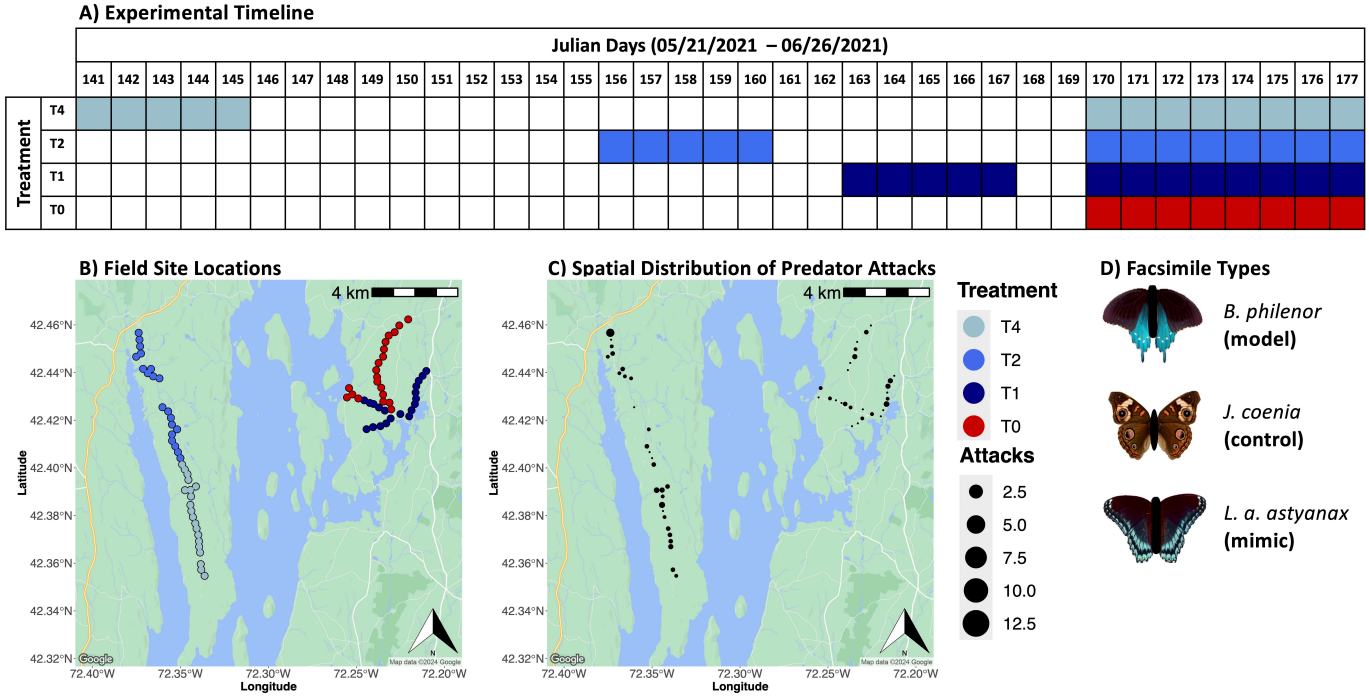

Figure 1. (A) Timeline for all temporal treatments in Julian days. All treatments were conducted between 21 May and 26 June 2021. (B) Map shows field sites at Quabbin Reservoir in central Massachusetts, USA, made using the ggmap and googleway packages [68,69]. Points represent sites containing 25 facsimiles of each species and colours represent distinct treatment. All asynchronous treatments are coloured in different shades of blue; synchronous treatment is shown in red. (C) Spatial distribution of predator attacks in each site; point size represents the number of attacks in a single site. (D) Phenotypes of each facsimile: *B. philenor* (toxic model), *J. coenia* (palatable control) and *L. a. astyanax* (palatable mimic).

the mimic and the palatable control were not treated with a Bitrex solution. Facsimiles were checked daily, and predation events were photographed and recorded as outlined in the training phase section.

(c) Assessing facsimile colour accuracy

Spectral reflectance measurements of the mimetic wing patches on the dorsal hindwings of facsimiles were compared against measurements from real butterfly wings to ensure colour accuracy. Detailed methods for facsimile construction are available in appendix I.I of the electronic supplementary material. Reflectance spectra were recorded for 10 facsimiles of each species (*B. philenor* and *L. a. astyanax*). For comparison, we took spectral reflectance measurements of 10 *L. a. astyanax* butterflies from the collections at the McGuire Center for Lepidoptera and Biodiversity within the Florida Museum of Natural History. Spectral reflectance measurements of the dorsal hindwings of male *B. philenor* butterflies, courtesy of Stavenga *et al*. [78], were used for comparison with *B. philenor* facsimiles. Facsimiles of *J. coenia* were analysed for colour accuracy in Kristiansen *et al*. [9]. No modifications were made to the design of these facsimiles during our study and additional spectral reflectance measurements were not collected. Measurements were taken using an Ocean Optics USB2000 fibre optic spectrometer with a bifurcating cable (R400−7-UV-vis Ocean Optics, Winter Park, FL) and a deuterium-halogen tungsten light source (Model MINIDT1000-027; Analytical Instrument Systems, Flemington, NJ). The spectrometer was calibrated with a Spectralon diffuse reflectance white standard (WS-1-SL; Labsphere, North Sutton, NH) before sampling each individual. The detection probe was positioned at a 45° angle relative to the surface of the butterfly wing or facsimile using a machined probe holder (Ocean Optics RPH-1).

To assess the accuracy of mimetic colour patches in artificial butterfly facsimiles, just noticeable differences (JNDs) were calculated for reflectance comparisons using the pavo package (v. 2.9.0) [79] (electronic supplementary material, figure S2). JND scores were calculated by estimating quantum catches using a tetrachromatic bird-vision model and receptor noise model to accurately calculate colour distances [80]. The bird-vision model for comparing facsimiles and real butterfly wings uses blue tit (*Cyanistes caeruleus*) cone sensitivities, representing the UV-type avian visual system, a blue-sky illuminant and a Von Kries transformation for green backgrounds [9]. For colour distance calculations, we followed methods presented by Hart *et al*. [81] and used relative cone abundances (UV = 0.37, S = 0.7, M = 0.99, L = 1). All comparisons were made at the same patch on the left dorsal hindwing of each sampled individual (electronic supplementary material, figure S2). JND values less than 1 indicate that two colour patches are visually indistinguishable in ideal conditions and JND values less than 3 are considered barely distinguishable, especially in visually complex natural environments [82,83]. Our comparisons of real wing and facsimile colour patches produced a JND value of 0.69 for *L. a. astyanax* and 1.42 for *B. philenor*, indicating that *L. a. astyanax* facsimiles are indistinguishable from real butterflies and *B. philenor* facsimiles are probably near indistinguishable from real butterflies, given that our experiment was conducted under natural conditions (electronic supplementary material, figure S2). These JND values are consistent with those found in experiments that used similar methods of assessing colour accuracy [9,23,82,84].

(d) Statistical analysis

(i) Training phase

We hypothesized that avian predators would learn to avoid chemically defended facsimiles of *B. philenor*, but not facsimiles of *J. coenia*, a common palatable butterfly, during our 4 day predation experiment. To test this hypothesis, we ran a generalized linear mixed model (GLMM) with a zero-inflated Poisson distribution using the glmmTMB package (v. 1.1.9) [85]. In our training phase model, we included the total number of predator attacks on facsimiles as the response variable and the species by experiment day interaction and transect as fixed effect variables. To account for spatial autocorrelation, we included a random effect of 'position' using the spatial exponential structure of the glmmTMB package. 'Position' is defined from a Euclidean distance matrix based on latitude and longitude coordinates of each field site and the variable 'group' was used to fit these coordinates in the model, following [85,86]. Alternative models, likelihood-ratio tests and Akaike information criterion (AIC) comparisons that support the models selected are shown in electronic supplementary material, table S3.

Transect was included as a fixed effect to test for spatial and temporal confounds across training phases. Our training phases were experimentally identical but occurred in different parts of the Quabbin Reservoir at different times. Because these training phases were experimentally identical, data were pooled to test the effect of transect, which captures both spatial and temporal variation, and to allow a sufficient sample size to run day-by-day pairwise contrasts. Residuals were evaluated using the DHARMa package (v. 0.4.6) [87]. Tests for dispersion, outliers, uniformity and zero inflation did not reveal significant deviations from assumptions. A zero-inflated Poisson model was chosen rather than a more informative negative binomial model due to low attack rates and the high occurrence of zeros in the dataset, which resulted in lack of convergence for the negative binomial model. We hypothesized that *B. philenor* would experience high attack rates on day 1 due to its novelty and large size, and that attack rates would decrease sharply on days 2, 3 and 4 as the proportion of educated predators increased. To test this, we ran pairwise contrasts with a Bonferroni correction for planned comparisons on experiment day for each species using the emmeans package (v. 1.10.2) [88]. Because our hypotheses are based on comparisons of experiment day within species, we also ran these models on each species separately to remove the interaction effects. Comparisons of model fit for models without interactions are shown in electronic supplementary material, table S8.

(ii) Testing phase

We predicted that avian predators would attack facsimiles of *L. a. astyanax*, the palatable mimic, significantly less than facsimiles of *J. coenia*, the palatable control when they learned to avoid the model one week prior to encountering the mimic, in accordance with the model first hypothesis, and that this protection for the mimic would break down over time. Finally, we predicted that predators would attack facsimiles of the mimic at a higher frequency relative to the control in the synchronous treatment because predators have not yet learned to avoid facsimiles of the model [32] and phenotypes are easier to distinguish when presented simultaneously [54].

To test these hypotheses, we fitted a GLMM with a zero-inflated Poisson distribution using the glmmTMB package in R (v. 1.1.9) [85]. In our testing phase model, we included the total number of predator attacks in each site as the response variable, the species by treatment interaction as a fixed effect and field site and field day (the date facsimiles were checked for predation) as random effects. We ran this model with and without the correction for spatial correlation described above and found no difference in model fit (chi-squared = 0, p-value = 1), so we proceeded with the simpler model. Alternative models, likelihood-ratio tests and AIC comparisons that support the models selected are shown in electronic supplementary material, table S4. Residuals were evaluated using the DHARMa package (v. 0.4.6) [87]. Tests for dispersion, outliers, uniformity and zero inflation did not reveal significant deviations from model assumptions. We ran planned pairwise contrasts with a Bonferroni correction for planned contrasts comparing attacks on the mimic and the control in each treatment using the emmeans package (v. 1.10.2) [88]. Directly comparing attack rates on facsimiles of *L. a. astyanax* and *J. coenia* in each temporal treatment allowed us to further control for spatial variation in predator foraging between our four transects. Finally, we ran a pairwise chi-squared goodness-of-fit test comparing attack totals on the model (*B. philenor*), the mimic (*L. a. astyanax*) and the control (*J. coenia*) in the synchronous treatment using the rstatix package (v. 0.7.2) [89]. Because our hypotheses are based on direct comparisons between the mimic and the control within each treatment, we also ran these models independently by treatment to test the main effect of species by treatment without interactions. Comparisons of model fit for models without interactions are shown in electronic supplementary material, table S9. Detailed methods for models without interactions for both training and testing phases are shown in appendix I.II of the electronic supplementary material.

3. Results

(a) Predator community analysis

During 2021, 12 660 observations of insectivorous birds at the Quabbin Reservoir were recorded in *eBird*, representing 48 species. Of those observations, 2592 (42 species) were recorded during our experimental time interval. Of our 80 field sites, 55 sites experienced predator attacks. Sites with predator attacks were distributed evenly across the four transects (11, 14, 16 and

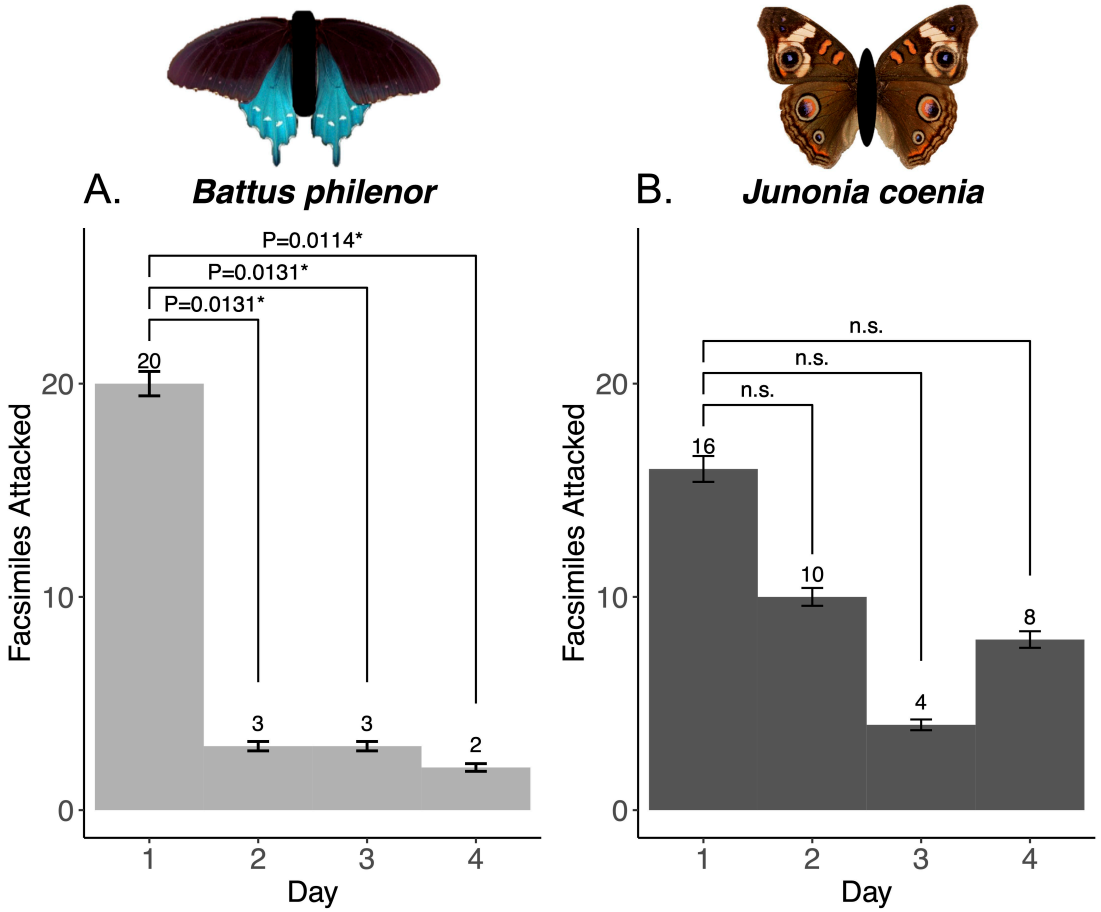

Figure 2. Total attacks on facsimiles of *B. philenor* and *J. coenia* by day; summed across training phases of asynchronous treatments. (A) Attacks on Bitrex-treated facsimiles of *B. philenor*. (B) Attacks on facsimiles of *J. coenia*, locally abundant, palatable control. Attack totals for each day are shown above each bar plot. Error bars show standard deviation in attack counts.

14 for T0, T1, T2 and T4, respectively), and the average number of predator attacks per site was 1.94 for the training phase and 1.76 for the testing phase. We found no significant spatial autocorrelation in predation events across 30 distance classes, indicating spatial randomness in predator behaviour in the Quabbin Reservoir (electronic supplementary material, table S2). Our kernel density analysis indicated that the 95% range boundaries did not overlap with the boundaries of Quabbin Reservoir for all insectivorous bird species found in the Quabbin Reservoir during the experimental window (electronic supplementary material, figure S3). Six fledgling events were recorded on *eBird* in 2021; all were recorded between 26 June and 22 July, after our experiment concluded. We found 24 observations of migratory insectivorous bird species, representing 0.93% of all observations during the experiment. These observations represent three species: bay-breasted warbler (*Setophaga castanea*), blackpoll warbler (*Setophaga striata*) and northern parula (*Setophaga americana*). Our analysis of BCS revealed no significant variation in community composition across the four temporal intervals of the experiment (p-value = 0.109; electronic supplementary material, figure S4).

(b) Training phase

In the training phase, we examined avian predator attack frequency on Bitrex-treated facsimiles of *B. philenor* (chemically defended model) and untreated facsimiles of *J. coenia* (known, palatable control) across three experimentally identical treatments conducted in different locations (figure 1) at different times (21–25 May, 5–9 June, 12–16 June). We recorded 66 avian attacks on 3000 facsimiles across 60 unique field sites, resulting in an overall attack rate of 2.2%. The control was attacked at a higher rate relative to the model (38 and 28 attacks, respectively). This finding is supported by a significant main effect of species in our GLMM (p-value = 0.04502; table 1). Attack rates on both species were higher on the first day of the experiment, consistent with previous studies demonstrating that naive predators will attack facsimiles more frequently. Attacks on both species decreased over time (i.e. as the proportion of educated predators increased), and our GLMM revealed that experiment day was highly significant (p-value = 3.906×10^{-5}). However, the species by experiment day interaction was not significant. Despite this non-significant interaction, our planned contrasts of experiment day within species showed that attacks on days 2, 3 and 4 were significantly lower than attacks on day 1 for *B. philenor* (p-value = 0.0131, 0.0131 and 0.0114, respectively; figure 2; table 1). There were no significant differences in pairwise contrasts of experiment day for *J. coenia*, suggesting that predators learned to avoid facsimiles of the toxic model species, but not the control. When we ran models without interactions, we found that the main effect of experiment day was highly significant for *B. philenor* (p-value = 3.906×10^{-5}; electronic supplementary material, table S5a) and marginally significant for *J. coenia* (0.06986; electronic supplementary material, table S5b). Results of our planned contrasts were the same for models with and without interactions. We found no significant effect of transect in either model (table 1).

Table 1. GLMM analysis with interactions for training and testing phases of the predation experiment. Planned pairwise contrasts are shown with Bonferroni *p*-value correction to adjust for planned comparisons. s.e. = standard error, d.f. = degrees of freedom, transect = experimental location (T4, T2, T1, T0), treatment indicates temporal delay treatment group (four weeks, two weeks, one week, synchronous). 'Position' is defined from a Euclidean distance matrix based on latitude and longitude coordinates of each field site and the variable 'group' was used to group these coordinates using spatial exponential structure.

a. training phase model with planned pairwise contrasts

model = glmmTMB(attacks ~ experiment day*species + transect + exp(site position + 0 | group)

zero Inflation: ~1

fixed-effect variable	**chi-squared**	**d.f.**		***p*-value**	**significance**
experiment day	23.0692	3		3.906×10^{-5}	***
species	4.0179	1		0.04502	*
transect	0.8252	2		0.66192	n.s.
experiment day: species	6.1573	3		0.10420	n.s.
planned pairwise contrasts with Bonferroni *p*-value adjustment					
contrast	**estimate**	**s.e.**	***Z*-ratio**	***p*-value**	**significance**
species = *B. philenor*					
day 1–day 2	1.897	0.619	3.064	0.0131	*
day 1–day 3	1.897	0.619	3.064	0.0131	*
day 1–day 4	2.303	0.742	3.105	0.0114	*
day 2–day 3	0.000	0.816	0.000	1.000	n.s.
day 2–day 4	0.405	0.913	0.444	1.000	n.s.
day 3–day 4	0.405	0.913	0.444	1.000	n.s.
species = *J. coenia*					
day 1–day 2	0.470	0.403	1.166	1.000	n.s.
day 1–day 3	1.386	0.559	2.480	0.0789	n.s.
day 1–day 4	0.693	0.433	1.601	0.6566	n.s.
day 2–day 3	0.916	0.592	1.549	0.7286	n.s.
day 2–day 4	0.223	0.474	0.470	1.000	n.s.
day 3–day 4	−0.693	0.612	−1.132	1.000	n.s.

b. testing phase model with planned pairwise contrasts

model = glmmTMB (attacks ~ species * treatment + (1|field site) + (1|field day)

zero Inflation: ~1

fixed-effect variable	**chi-squared**	**d.f.**		***p*-value**	**significance**
species	0.8598	1		0.3538	n.s.
treatment	5.1022	3		0.1645	n.s.
species: treatment	6.8610	3		0.0764	n.s.
planned pairwise contrasts with Bonferroni *p*-value adjustment					
contrast	**estimate**	**s.e.**	***Z*-ratio**	**p-value**	**significance**
treatment = four weeks					
J. coenia–*L. a. astyanax*	−0.4684	0.505	−0.927	0.3538	n.s.
treatment = two weeks					
J. coenia–*L. a. astyanax*	−0.4347	0.544	−0.799	0.4243	n.s.
treatment = one week					
J. coenia–*L. a. astyanax*	−0.0103	0.560	−0.0118	0.9853	n.s.
treatment = synchronous					
J. coenia–*L. a. astyanax*	1.3743	0.592	2.320	0.0203	*

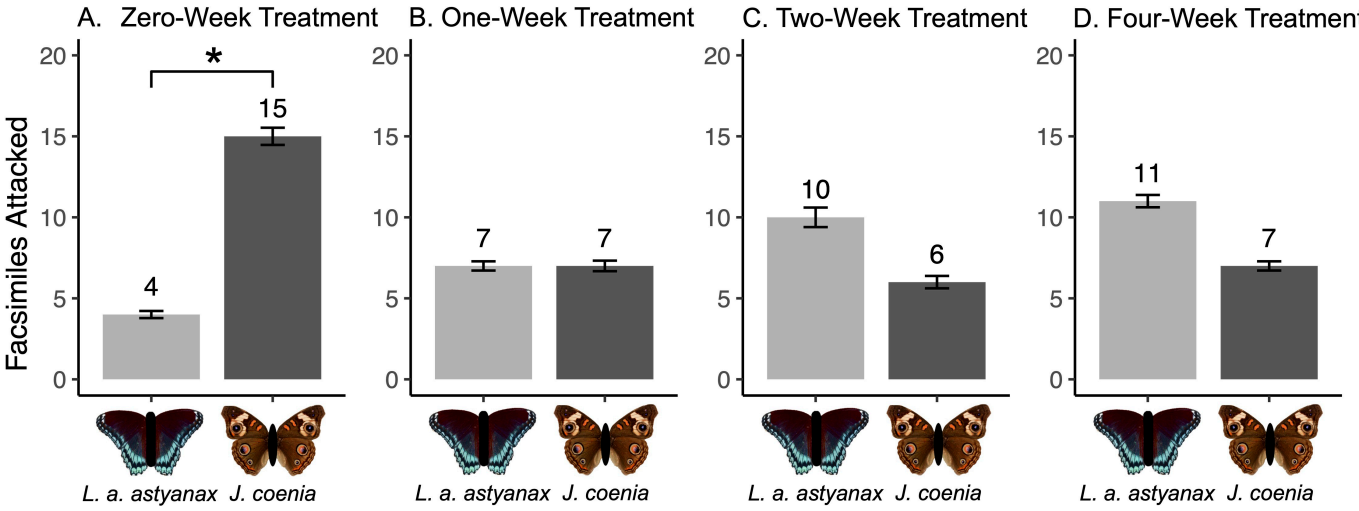

Figure 3. Total attacks on facsimiles of *L. a. astyanax* (palatable mimic) and *J. coenia* (locally abundant, palatable control) for all testing phase treatments. Attack totals on facsimiles are shown above each bar plot, and error bars show standard deviation in attack counts.

(c) Testing phase

In the testing phase, we recorded 75 avian predator attacks on 4500 facsimiles across 80 field sites, with an overall attack rate of 1.64%. Surprisingly, the mimic was attacked equally, if not more frequently than the control in all asynchronous treatments, indicating no protection against predation for palatable mimics (figure 3B–D). However, both the model and the mimic experienced reduced attacks relative to the control in the synchronous treatment (6, 4 and 15 attacks, respectively). Comparisons of attack totals by species and treatment indicate a species by treatment cross-over interaction, though this interaction was only marginally significant in our GLMM (p-value = 0.0764; table 1). When we examine this model in greater detail with planned contrasts, we found no significant difference in attacks on *L. a. astyanax* and *J. coenia* in the asynchronous treatments (figure 3B–D; table 1), and a significant difference in attacks on *L. a. astyanax* and *J. coenia* in the synchronous treatment (p-value = 0.0203; figure 3A; table 1). In our models without interactions, we also found a significant difference in attacks on the mimic and the control in the synchronous treatment (p-value = 0.02439) and no significant difference in the asynchronous treatments (electronic supplementary material, table S6). Finally, our pairwise chi-squared goodness-of-fit test showed a significant difference in attacks on the model (*B. philenor*) and the control (*J. coenia*) (p-value = 0.0495), and the mimic (*L. a. astyanax*) and the control (p-value = 0.0116), but no significant difference in attacks on the model and the mimic (electronic supplementary material, table S7).

4. Discussion

Frequency dependence and geographic sympatry maintain Batesian mimicry in nature by teaching predators what not to eat [5,6,10,23,27,45,50]. However, the role of phenology in driving predator foraging strategies and its ultimate consequences for maintaining mimicry have not been experimentally tested. The model first hypothesis suggests that mimics could benefit from relaxed selection by displacing their emergence times, relative to the model, to give predators an opportunity to learn, recognize and avoid the warning signal of an unpalatable model [29,31,32,35].

Our experiment investigated how predation on mimic facsimiles was influenced by the time since exposure to an unpalatable warning signal. We predicted that predators would learn to avoid Bitrex-treated facsimiles of the chemically defended model species, *B. philenor*, but not the palatable control, and then generalize this avoidance to palatable facsimiles of *L. a. astyanax*, its imperfect Batesian mimic. Specifically, we predicted greatest protection from predation for the mimic when birds learned to avoid the model one week before encountering the mimic, consistent with previous research supporting the model-first hypothesis [31]. We also predicted that protection for mimics would decay over time as predicted by classical conditioning theory [6]. Furthermore, because theory predicts that synchronized emergence dilutes predator learning [32] and predators are better able to distinguish between two similar phenotypes when they are presented simultaneously [54,55], we predicted that there would be weak protection for the mimic under conditions of temporal synchrony without model-first occurrence.

Consistent with our first prediction, while attack rates on both species declined over 4 days, predators showed greater learned avoidance of the model (figure 2; table 1). However, we cannot rule out the possibility that birds did learn to avoid both the model and the control, due to the non-significant species by day interaction. More work is needed to understand the relative effects of distastefulness and wasted effort in driving learned avoidance in wild predators. We also observed high attack rates on *B. philenor* on day 1, consistent with their increased conspicuousness relative to our controls [59]. Surprisingly, our testing phase models suggest that birds did not generalize learned avoidance of the toxic model to facsimiles of the mimic when models and mimics occurred asynchronously (figure 3; table 1). However, our planned contrasts within treatments and our GLMMs without interactions showed significantly lower attacks on *L. a. astyanax*, relative to *J. coenia*, in

the synchronous treatment, suggesting that birds only generalize learned avoidance of the model when models and mimics are present simultaneously (figure 3; table 1; electronic supplementary material, table S6). This finding is supported by our chi-squared test, which shows that both models and mimics benefited from protection against predation in the synchronous treatment (electronic supplementary material, table S7). Our results are consistent with the idea that predators put more weight on current information when making foraging decisions, suggesting that temporal synchrony may be important for mimetic protection. However, more work is needed to fully understand how temporal synchrony functions to maintain mimicry in nature.

Our experiment tested predation on an imperfect mimic in a field site near the model's range edge, suggesting that temporal synchrony may be important in the context of imperfect mimicry or in environments where the model's presence is highly unpredictable. Interestingly, previous work conducted in Central Illinois found that some avian predators avoided mimics of *B. philenor* when *B. philenor* was temporally absent [90]. However, this experiment was conducted in a region where *B. philenor* is highly abundant, while our experiment was conducted in Central Massachusetts, where *B. philenor* is extremely rare. Thus, our results highlight the potential for patterns of geographic sympatry to influence predator foraging strategies across the model's range, leading to geographic differences in the relative importance of temporal synchrony in maintaining mimicry complexes. Previous work using computer-based experiments to determine the selective advantage of different phenological strategies found that while aposematic models benefit from educating predators quickly (i.e. model first occurrence), mimics may benefit most from synchronized emergence, where models and mimics are presented to predators at random, as opposed to only models followed by a mix of models and mimics. This synchronized emergence can, therefore, create unpredictable learning conditions for predators [30]. If so, overlapping flight times for models and mimics could maintain imperfect mimicry in geographic areas where the annual abundance of both models and mimics is highly unpredictable or varies substantially throughout the flight season [45]. Overall, our results suggest that temporal synchrony may benefit mimics by relaxing selection on mimics that emerge simultaneously with their model when predators put more weight on current information [19,20,22,50,91–93].

Although our experiment was not designed to investigate different models of predator cognition, it is informed by our understanding of the factors governing predator foraging behaviour. Müller's [94] original description of mimicry dynamics assumed that predators need to sample a fixed number (n) of unpalatable prey to learn, recognize and avoid warning signals. However, more realistic Pavlovian models [14,28] demonstrate that predator behaviour is more complex and that mimicry dynamics are highly sensitive to assumptions about learning and memory. Predators in the process of learning may cease sampling imperfect mimics because the immediate pay-off and future value of the information are low [93]. Theoretical models of dynamic learning indicate that when information about prey profitability is constantly changing, less weight should be given to past information and predators should rely on current information when making foraging decisions [95]. Therefore, if learning is not complete, optimal foraging decisions might be governed largely by trade-offs between investing in more sampling to learn about prey types (i.e. exploration) versus relying on current information (i.e. exploitation). This mechanism could explain the results of both our synchronous and asynchronous treatments. In the former, sampling by naive predators would result in frequent encounters with unpalatable prey types and protection for the imperfect mimics. In the latter, predators may experience time-dependent forgetting or reversion learning due to ongoing exploration or additional sampling leading to a lack of protection for the imperfect mimics.

Additionally, the strength of prey unpalatability could influence the duration of aversion learning [6]. If a negative stimulus stronger than Bitrex were used, we might have seen greater, more persistent avoidance of the palatable mimic when presented asynchronously with the model. Future work should explore how variant unpalatability affects the duration of learned avoidance of aposematic signals in natural environments. Our results highlight that predator learning and foraging can drastically change the predicted dynamics of mimicry in nature. Ultimately, more work is needed to understand how predator cognition drives predator foraging decisions and its consequences for the fitness of imperfect mimics in nature under different conditions.

Given that our predator community analyses revealed no spatial autocorrelation in attack rates across our field sites (electronic supplementary material, table S2) and demonstrated that all facsimiles were placed in ideal avian habitat within predator range boundaries (electronic supplementary material, figure S3), we can assume that predator community composition did not vary significantly across our field sites. Our training phase model showed no significant effect of transect, our proxy for space and time, after controlling for spatial correlation in the model, further indicating that predator foraging behaviour did not vary spatially (electronic supplementary material, table S3). However, as with all field experiments, we cannot completely control for potential confounding effects of variation in predator behaviour and availability of alternative prey across our field sites. Our experiment did not overlap with avian fledgling dates; however, we did find a small number of migratory birds present. All three migratory species are expected to migrate out of Massachusetts during the first week of June, indicating that our testing phase was probably not affected by an influx of naive birds. Therefore, we do not expect the presence of these migratory birds to influence the validity of our results. Our analysis of BCS revealed no temporal variation in predator community structure, indicating that the bird community that learned to avoid *B. philenor* facsimiles in the training phase was probably the same community that did not avoid the mimic, *L. a. astyanax*, in the testing phase (electronic supplementary material, figure S4).

Attack rates on facsimiles in our experiment, while lower than similar experiments carried out in tropical environments [23,82], are consistent with other field predation experiments that only assessed avian predation [9,84]. The low attack rate is probably a consequence of both our conservative predation scoring metrics and the absence of a food reward incentive. However, including a food reward would have limited our ability to focus on the avian predator community, as these experiments typically record predation as the absence or partial absence of a food reward [73,96]. Furthermore, while variation

in hunger level across the predator community may have driven differences in attack rates, as a predator's willingness to consume toxic prey often varies with the availability of alternative prey and the nutritional value of the toxic prey species [15,16,49], providing a nutritional incentive to wild predators would have altered the underlying nutritional status of the predator community.

Most previous studies of phenology in the context of mimicry support the model-first hypothesis [34,38–40]. However, few have disentangled the roles of model first occurrence and temporal synchrony. Our experiment gives insight into the potential role of temporal synchrony in maintaining mimicry complexes and highlights model first occurrence (i.e. emergence order) and temporal synchrony (i.e. overlapping flight times) as distinct, non-mutually exclusive ecological predictions of mimicry systems. More work is needed to disentangle the relative importance of these two predictions and understand how model first occurrence with temporal synchrony may benefit mimics under certain ecological conditions.

Ethics. This work did not require ethical approval from a human subject or animal welfare committee.

Data accessibility. All data and corresponding analyses are publicly available at [97]. Data from eBird analyses can be downloaded at ebird.org. Supplementary material is available online [98].

Declaration of AI use. We have not used AI-assisted technologies in creating this article.

Authors' contributions. A.E.R.: conceptualization, data curation, formal analysis, investigation, methodology, project administration, visualization, writing - original draft; I.N.: data curation, writing—review and editing; J.H.: data curation, writing—review and editing; L.D.: data curation, writing—review and editing; A.E.: data curation, writing—review and editing; D.F.: data curation, writing—review and editing; C.F.: data curation, writing—review and editing; B.F.: data curation, writing—review and editing; J.M.: data curation, writing—review and editing; M.M.: data curation, writing—review and editing; T.G.H.N.: data curation, writing—review and editing; P.M.B.: formal analysis, methodology, resources, writing—review and editing; T.N.S.: methodology, resources, writing—review and editing; S.P.M.: conceptualization, funding acquisition, project administration, resources, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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